# HYBRIDIZATION AND INTROGRESSION IN QUERCUS ALBA[1]

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THE MOST OBVIOUS and most frequent variability in *Quercus alba* L., white oak, is intrinsic; that is, it occurs as random genetic variance, ecotypic or ecophenic variation, as discussed by Baranski (1975). In addition, a significant, although relatively minor, component of the variation is due to hybridization and localized introgression with eleven other white oaks of the subgenus QUERCUS (*Lepidobalanus*) which are sympatric with *Q. alba* in various parts of its range.

During the 27 years since Palmer (1948) summarized the history of American hybrid oaks, there has been continued interest in various crosses or introgressed populations. Most of the studies have been based on gross morphology of natural populations or seedling progeny, and there is still a need for analyses of other characteristics, as well as for experimental work. One of the most perplexing gaps in our knowledge is the need for an understanding of the barriers that either effectively maintain the individual species or are at times weaker and allow limited hybridization and introgression.

The intent of this paper is to summarize the information now available and to answer the basic question of just how important hybridization and introgression are as contributors to the total variation in *Quercus alba*. Field studies were made from southeastern Canada and New England to Illinois and south to Florida and Texas from 1965 to 1973. Herbarium material was examined from A, DUKE, FSU, GA, GH, HAM, IA, ILL, IND, KANU, KY, MICH, MIN, MISSA, MO, NCU, NCSC, OS, PAC, PH, SMU, UARK, US, WISC, and WVA. Acorns from numerous labeled hybrid trees from the Arnold Arboretum and from natural populations were planted in the North Carolina State University greenhouse and the seedlings analyzed. The collections made by M. J. Baranski during 1969 and 1972, as well as his intimate knowledge of the species, have been invaluable to this study. Voucher specimens for the research are the annotated specimens in the herbaria indicated above plus my collections and those of M. J. Baranski deposited in NCSC.

## THE WHITE OAK SYNGAMEON OF EASTERN NORTH AMERICA

Gene exchange occurs or at least has the potential for taking place among nearly all species of subg. QUERCUS in eastern North America (albeit to a very limited extent in most cases), and the species can be

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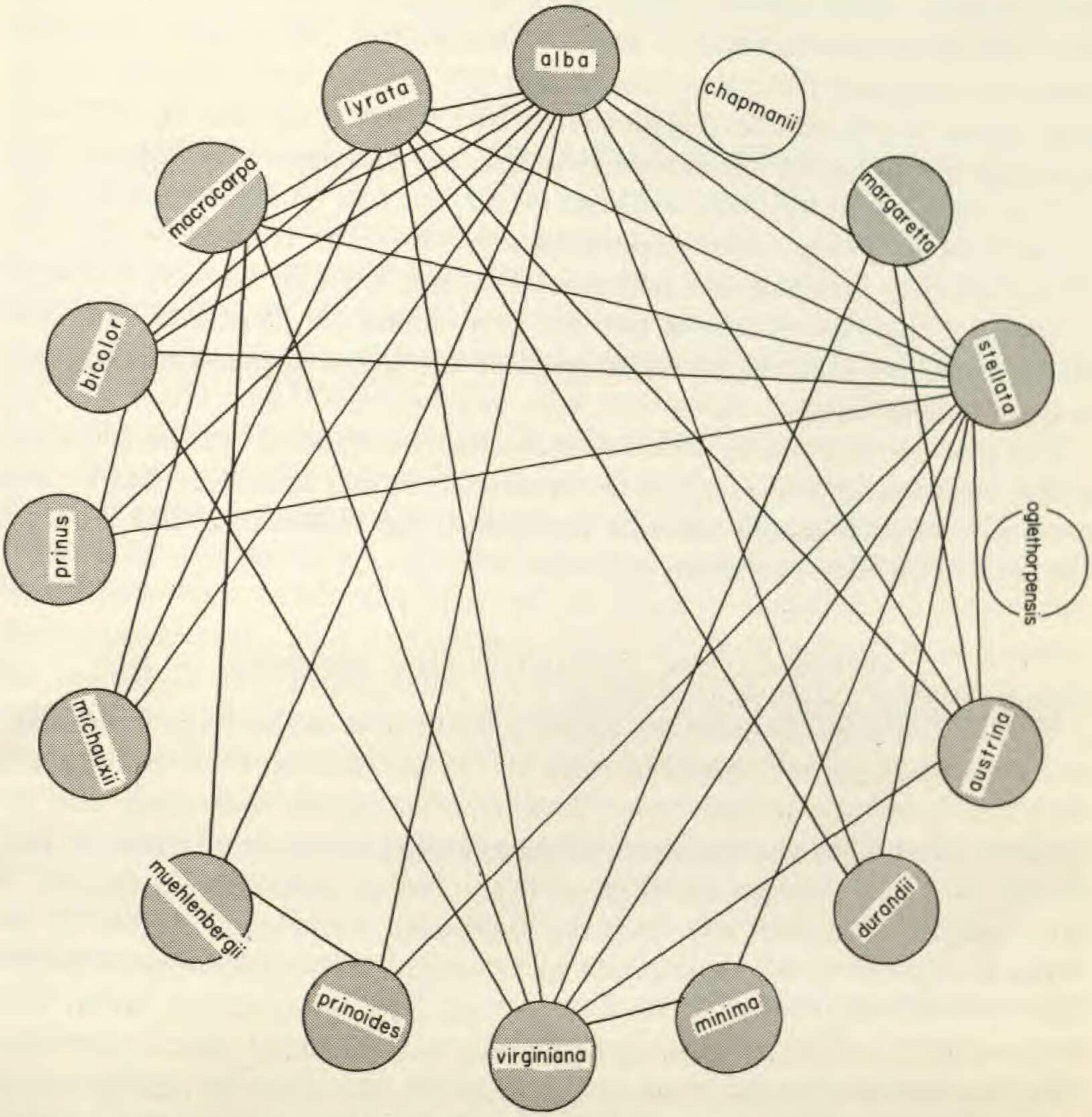

FIGURE 1. The white oak syngameon of eastern North America (shaded areas).

thought of as comprising the most inclusive breeding group or syngameon (Grant, 1971). The syngameon pictured here (FIGURE 1) is arbitrarily limited to the indigenous white oaks that occur east of Oklahoma and Texas. In actuality it is more inclusive because of crosses with *Quercus robur*, which is cultivated in the East, and *Q. gambelii* and *Q. havardii*, which are more western. Various crosses with these more western species form a connecting link between the eastern and western white oaks (Tucker, 1961).

Only the crosses involving *Quercus alba* have been included in this study. The other crosses indicated (FIGURE 1) are from the literature (Palmer, 1948; Correll & Johnston, 1970), from my collections, or from herbarium specimens examined.

It is interesting to note that *Quercus alba* and *Q. stellata* cross with more species than does any other member of this group. This may possibly reflect the relatively broad distribution and ecological amplitude of these species, which permit them to be sympatric with so many others. The lack of certain hybrids is equally interesting. No crosses involving either *Q. chapmanii* or *Q. oglethorpensis* are known, and for this reason they cannot at present be considered part of the syngameon. In addition, there are a number of species pairs which are frequently sympatric, but between which hybrids have not been found, such as *Q. bicolor–michauxii*, *Q. macrocarpa–prinus*, and *Q. michauxii–prinus*. The reason for the lack of hybrids may be either the presence of strong intrinsic barriers or merely the fact that hybrids have not yet been found or identified. In view of the extensive crossing of other species, the latter explanation appears to be the more likely.

The pattern of crossing within the subgenus substantiates the inclusion of the evergreen species, such as *Q. virginiana*, in this subgenus, but it does not lend support to the sections recognized by either Trelease (1924), Camus (1936–39), or Rehder (1940).

## RECOGNITION OF WHITE OAK HYBRIDS

The basic prerequisite for recognizing hybrids is a thorough knowledge of the intrinsic variation within each of the parental species, particularly that due to ecophenic and ecotypic differences, stump sprouting, and juvenility, as well as to stress morphology created by extreme climatic conditions or insect damage (Muller, 1941). Once a total species concept is acquired, hybrid forms can then be recognized with some degree of assurance. However, the designation of hybridity and attribution of parentage are still only opinions based on comparative morphology, often with circumstantial evidence from associated species, ecology, and geography. There is seldom any real proof of the proposed hybridity in nature.

It may be assumed that a first generation hybrid will be more or less intermediate between the parent species in nearly all features — leaves, twigs, acorns, bark, phenology, fall coloration, and ecology. It must be remembered, however, that all of the species are variable and the different forms of the parental types could yield hybrids with slightly different characteristics. There is also the possibility of dominance or epistasis, morphological irregularities, or transgressive segregates.

Continued generations ($F_2$, etc.) tend to segregate somewhat, and the segregates are often similar to and difficult to distinguish from the parental species. Oaks, in general, have been thought to be rather self-incompatible (Irgens-Moller, 1955; Piatnitsky, 1960), so that selfing would be rare. On the other hand, there is evidence that indicates considerable selfing, at least within *Quercus alba* and hybrids. Isolated trees beyond the effective pollination range of other trees seem regularly to bear large numbers of acorns. Although the effective pollination range for oaks is not precisely known, such normal fruit production would indicate selfing, assuming, of course, that the acorns were not all of hybrid or apomictic origin. The pollen of oaks is small (ca. $35 \times 40$ μm.), and judging from work done with pines (Colwell, 1951), the effective pollination range would probably not exceed 200 meters. In addition, the various progeny tests (Allard, 1932, 1949; Bartlett, 1951; and the analysis of *Q. alba* × *bicolor* reported here) also tend to substantiate selfing and segregation. However, since all of the trees used in these various studies were open grown, one could argue that the individual progeny considered to be "segregates" were in fact the result of backcrosses to the parental species. Without definitive information on the relative degree of self-incompatibility in white oaks, I am assuming that at least some selfing and segregation occurs regularly in the natural populations of the eastern white oaks.

When introgression occurs, there is developed a more or less complete bridge across the morphological and ecological gaps between the two parents, depending upon whether the backcrossing is unilateral or reciprocal. It may then be impossible, at least locally, to recognize any discontinuity between parents and hybrids or to identify correctly certain individuals as backcrosses. All features seem to vary independently, and techniques such as the use of a hybrid index or pictorialized scatter diagrams (Anderson, 1949; Goodman, 1966, 1967) or a discriminant analysis (Ledig *et al.*, 1969) must be employed to analyze complex hybrid populations and detect the subtle "trickle" of genes from one species into another. Differential survival of introgressed genes that affect nonmorphological traits may be nearly impossible to demonstrate. In fact, some of the breadth in ecological amplitude in many species could possibly be due to introgression rather than to something entirely inherent within the species. Therefore it is quite likely that the ecological effects of introgression extend beyond the range for which there is morphological evidence of hybridization. This brings up an interesting and unanswered question. Is the very broad ecological amplitude of white oak a result of introgression with eleven other species, or is it an intrinsic feature which allows such widespread crossing? This needs to be investigated.

White oak hybrids exist at various levels of frequency and importance in the natural populations. The lowest level is represented by a single tree, presumably an $F_1$, which is fairly easily recognized and whose parentage is readily surmised. Such obvious hybrids often attract local interest, and a herbarium will sometimes contain specimens from one tree that have been collected over many years by many botanists. These numerous herbarium specimens often give a false impression of the frequency of the hybrids in nature. A higher level is represented by a few $F_1$ or $F_2$ hybrids, some segregation products, backcross types, or all of these. These again are very local trees, which may have very little or no effect on the variation of white oak in the immediate area. At the other extreme is the hybrid swarm which is a complex mixture of parental forms, $F_1$ hybrids, or successive generations, including segregation products, introgressants, or crosses between any of these; or it may be an extensive introgressive population developed through repeated backcrossing with one or both parental species. I think the distinction between "hybrid swarm" and "introgressive population" is mainly academic and generally impossible to make in nature. Either situation may be quite local or may cover rather extensive areas and heighten the variability of white oak in the area. The obvious hybrids in such a population may have been identified and represented in herbaria, but the subtle segregates or introgressants have normally passed as one of the parental species.

The nature of the differences between the parental species increases the difficulty of recognizing or analyzing hybrids. Most differences are quantitative, and in some cases the species are already quite similar. As Palmer (1948) indicated, "the facility and certainty with which any natural hybrid can be identified is in inverse ratio to the similarity of the parent species." This is less of a problem when dealing with hybrids of *Quercus alba*, for the presence of rather loose or appressed branched hairs on the abaxial surface of the leaves is an almost certain clue to hybridization. Nine of the eleven species with which it crosses are rather densely pubescent, and the hybrids maintain a certain number of these hairs. Distinguishing which one of the nine possible parents is involved often becomes more difficult.

Since the form and density of hairs on the abaxial leaf surface is so important, a brief explanation is needed regarding the two main types of trichomes on mature leaves. The more conspicuous (at 10–15×) is a branched type ("non-glandular," according to Dyal, 1936). This type may be erect and "loose" or appressed, sessile, or pedicellate, and it may consist of 2 to 15 branches. The size, color, form, and number of branches are often quite characteristic of certain species. This is the more important trichome type in the recognition of hybrids, since it is common on all species under consideration here except *Quercus alba*, *Q. austrina*, and *Q. robur*. The second type is a stellate hair which is minute, generally appressed, and much less conspicuous except at a magnification of about 40×. These hairs, which give the impression of being somewhat viscid, were designated as "glandular hairs" by Dyal (1936). They are of little diagnostic value.

There is a need for new criteria in the study of eastern white oak hybrids. The chromosome number of $n = 12$ (Duffield, 1940) is the same for all species, and only slight differences in size and morphology of chromosomes (Stebbins, 1950) occur. Although no intensive cytological studies have been conducted on eastern white oak hybrids, this technique is not expected to be of great help. Sax (1930) found no significant differences in pollen sterility between different species and hybrids, but SEM studies of pollen grains may be worth investigating. Chemical analyses may add a new dimension, as indicated by Li and Hsiao (1974), to the investigation of hybrids and introgressed populations and should be made.

## ECOLOGICAL CONDITIONS OF HYBRIDITY

Hybrids are found primarily in (1) marginal, (2) intermediate, or (3) disturbed or open habitats. The conditions of these three habitats may, and often do, occur in combination. The disturbed, intermediate habitat is certainly the most frequent site for white oak hybrids.

Palmer (1948) observed that "hybrids are most likely to occur in nature along the margins of the range of one of the parent species where one is locally rare and the other abundant." His general principle stated that "other factors being equal, the chance for the production of natural hybrids between compatible species increases in proportion to the numerical inequality of the parent species in the immediate vicinity." This is generally true if "range" is interpreted to be "ecological" in local physiographic situations as well as "geographical" in terms of total distribution. Hybrids may be found at the margins of the geographical range (FIGURES 15, 16), but they are more frequently found at the margins of the ecological range. Palmer's explanation for this marginal position was based on relative pollen frequencies; i.e., "the chance of the rare parent being pollinated by one of its own kind" is less than "the chance of its pistillate flowers being fertilized by the wind-borne pollen of the dominant species." This assumes some degree of self-incompatibility as well as only weak incompatibility of foreign pollen. There is obviously a balance between these two mechanisms which allows the hybrids to form in these marginal situations.

In addition to this differential pollination, another possible explanation for the marginal location of hybrids may be the greater ability of the hybrid to compete in an area of stress for one of the parents. Theoretically, in an area where both parents are common in a closed community, there would be maximum competition or other interactions from the two species upon the establishment and development of the hybrid. Under such conditions hybrids are rare. However, a species at the edge of its range is not only less frequent, but under stress conditions its seedlings are at a selective disadvantage and it is not able to exert maximum competition against hybrids. The hybrids, presumably more like the dominant parent, are adaptively superior to the marginal species and can compete more favorably in such a situation.

The concept of the "hybridized habitat" has been thoroughly discussed by Anderson (1948, 1949) and by Grant (1971). It is interpreted here to mean "intermediate" or an "array of intermediate conditions" between the optimal habitats for the two parental species. In the case of *Quercus alba* and related species, the intermediacy is primarily in soil moisture or total moisture balance, soil texture, and soil pH. Relative shade tolerance may also be a factor. In certain habitats and regions, related species seemingly co-exist with white oak. But as pointed out above, both parental species exert maximum competition against the hybrid in such an apparently sympatric situation. Examples of apparent ecological sympatry are infrequent, however, since most related species that are geographically sympatric with white oak align themselves along the complex ecological gradient, with the optimum for each species at a slightly different point and with either no overlap or varying degrees of overlap between the ecological ranges of each. Anemophilous species can easily be within effective pollination range and yet be ecologically allopatric, even with a relatively short effective pollination range. The more narrow the ecological amplitude and the greater the difference between the ecological requirements of the parental species, the greater the likelihood is for a rather broad intermediate habitat in which neither parental species is very common. This concept also assumes that no other species is dominant in this intermediate habitat to the exclusion of both parents and hybrids. In such instances of ecological allopatry, an intermediate habitat is ideal and most often necessary for the survival of the $F_1$. Backcrosses and segregates have a better chance of occupying either the same habitat as the more similar parent or one of the various niches in the "hybridized" habitat *sensu* Anderson (1948, 1949).

In limited areas of overlap between the ranges of the species along the ecological gradient, the hybrid is likely to compete favorably, not only because of the intermediacy of its genotype and ecological requirements, but also because one or both of the parental types are on the margin of their ecological ranges and are therefore less competitive, as discussed above.

Although hybrid acorns are probably formed occasionally throughout the area of geographical sympatry between species, undisturbed, closed forests contain the parental species, with only a rare surviving hybrid or none at all except in the marginal or intermediate situations described above. In contrast, disturbed or open habitats are frequent locations for the survival of white oak hybrids. The survival of seedlings is obviously greater in areas where there is less interspecific competition and weaker habitat selection. Certainly as long as the eastern white oaks have existed there have been habitats repeatedly disturbed by natural agencies, and man probably has contributed to these during the past few thousand years. As modern man continues at an even faster pace to clear and develop the land, to overgraze, and to overcut, open as well as hybridized habitats will continue to increase. On the other hand, there is no strong evidence to indicate that white oak hybrids are now any more frequent than they were when first described (Engelmann, 1877; Trelease, 1924; Palmer, 1948). In very few populations is there evidence that hybrids are in greater relative abundance in the seedling and sapling class than in the older canopy class.

## WHITE OAK HYBRIDS

*Quercus alba* crosses naturally with eleven other species of the subg. QUERCUS (*Lepidobalanus*) (FIGURE 2). The arrangement of the species in FIGURE 2 is not meant to indicate relationships, but rather to show a trend from the fewest crosses (3) at the top to the most (8) at the botton. Within the twelve species, *Q. alba* crosses with the most. It is placed at the center merely for emphasis. *Quercus durandii* is included here with *Q. austrina*, as will be discussed later.

Seven of the eleven crosses with *Quercus alba* have been given binary names by such authors as Schneider, Trelease, and Palmer. The others have been designated by formula only. Since there is no unanimity of

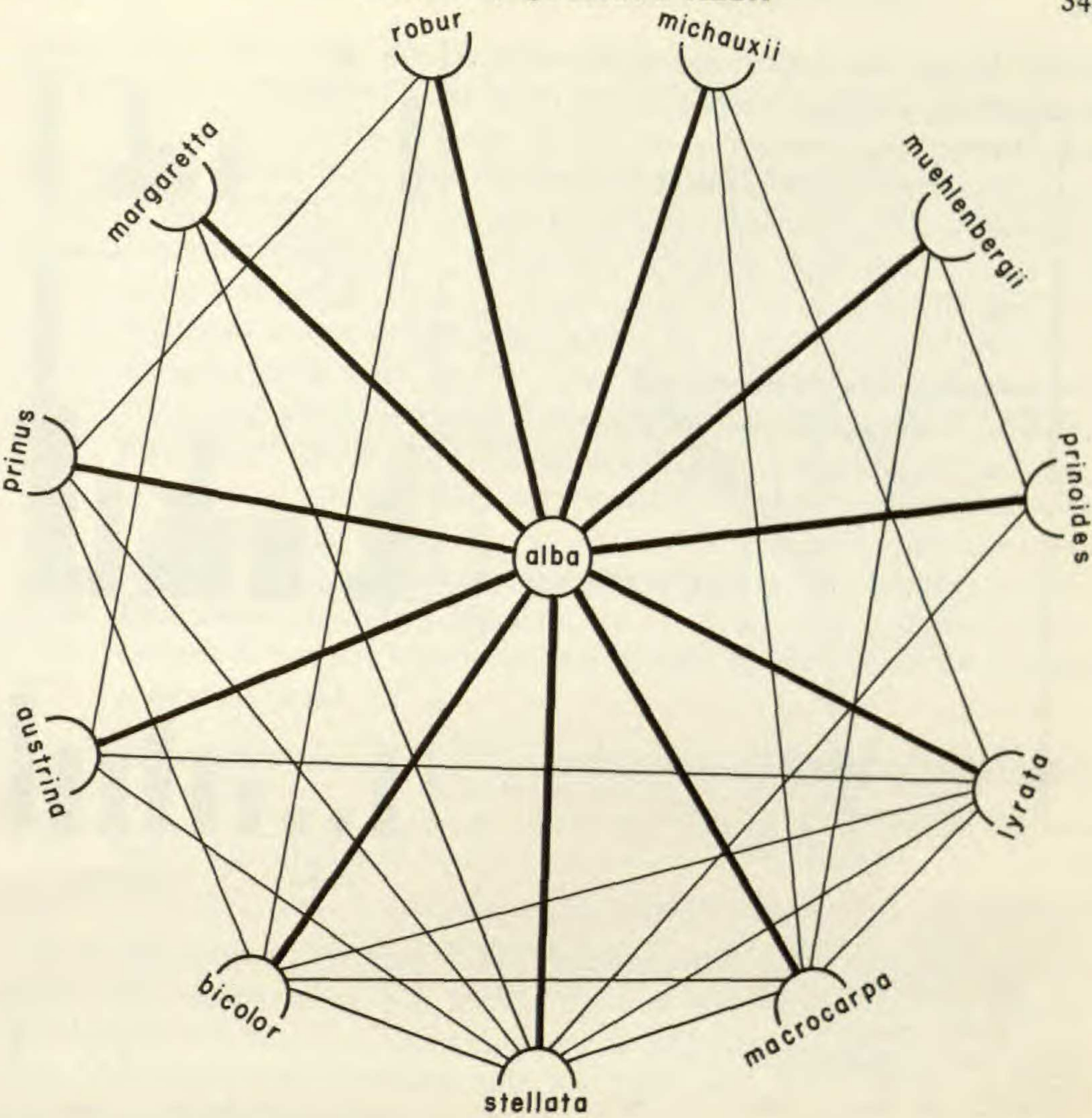

FIGURE 2. Natural hybridization between the eastern white oaks that cross with *Quercus alba*.

opinion regarding the preferable nomenclatural method for naming hybrids (Little, 1960; Rowley, 1961, 1964; Grassl, 1963), I prefer to be consistent throughout and to designate all hybrids by formula with the epithets in alphabetical order. None of the hybrids form large distinct populations or in any way resemble natural species.

Without direct proof of hybridity, the best evidence of hybridization is (1) a demonstration of morphological intermediacy and recombination in nearly all characters analyzed, (2) progeny tests, and (3) a comparison between the natural putative hybrids and those made artificially. Relying primarily on the first of these, analyses of populations (using the hybrid index or pictorialized scatter diagram methods of Anderson, 1949) were made based on various features of the leaf, acorn, twig, bark, and ecology, depending upon the particular cross and the character differences between the putative parents. Foliar features alone were used to analyze the progeny grown in the greenhouse.

The leaf offers the most obvious clue to hybridity, but features of the

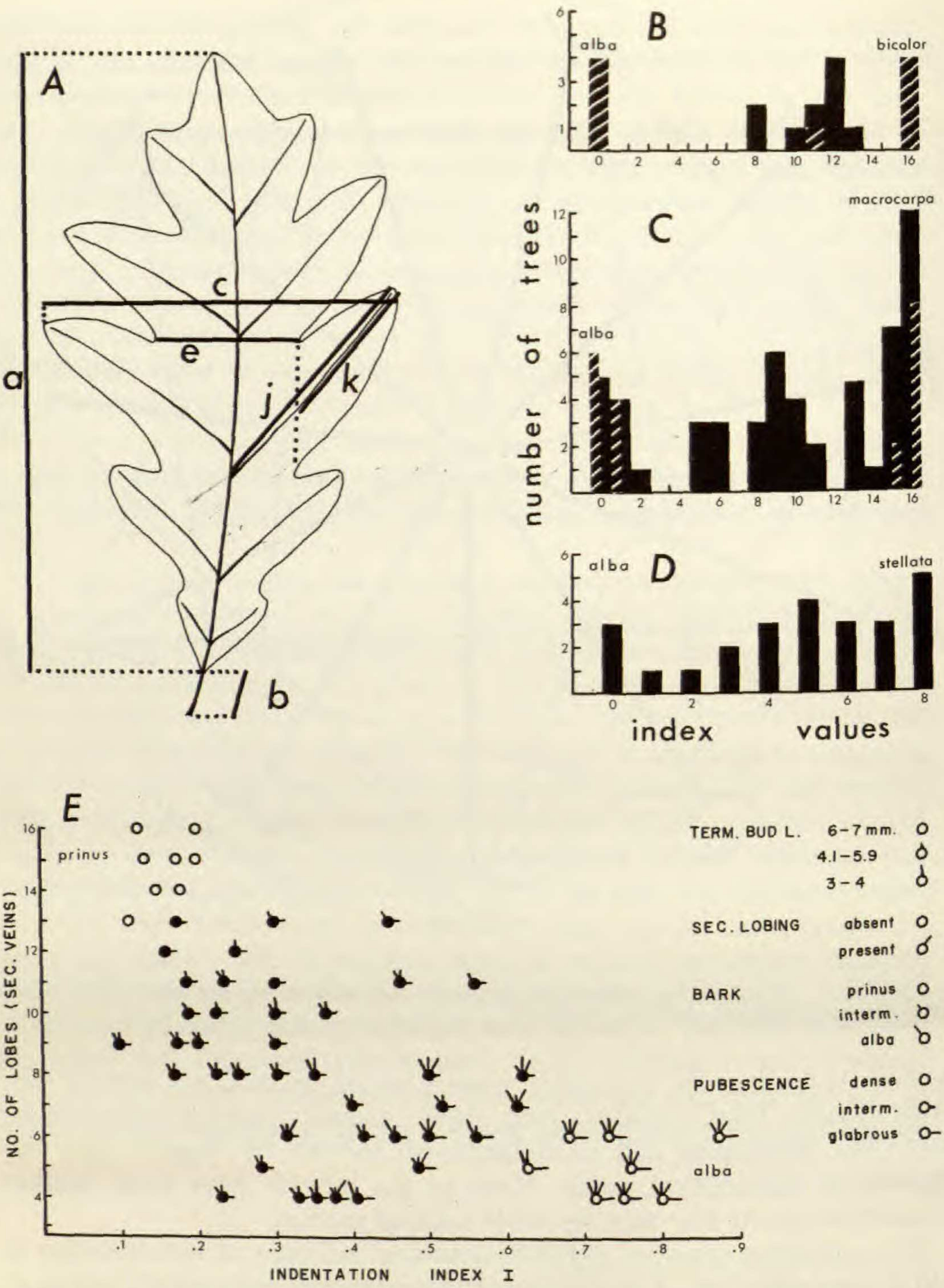

FIGURE 3. Analysis of variation. A, Measurements taken of leaf form (a = length of blade; b = length of petiole; c = width of leaf at widest point; e = intersinus width nearest widest point; j = length of longest lobe from base of vein; k = length of longest lobe from line between sinuses). B, Mature *Quercus alba*, *Q. bicolor*, and the hybrid tree growing at the Arnold Arboretum (hatched bars); progeny from the hybrid tree (solid bars). C, Hybrid population from Livingston County, Michigan (solid bars); typical *Q. alba* and *Q. macrocarpa* from southeastern Michigan (hatched bars). D, Hybrid population (*Q. alba* × *stellata*) from San Augustine County, Texas. E, Hybrid population (solid circles); typical *Q. alba* and *Q. prinus* (open circles); all from Wake County, North Carolina.

acorn, twig, and bark are of great diagnostic value and should always be used when available. The type and relative density of trichomes on the abaxial leaf surface are one of the most important characters. The following variables were used for analysis of leaf form (FIGURE 3A):

1. Length of blade (a).
2. Length of petiole (b).
3. Width of leaf at widest point (c).
4. Length/width ratio (a/c).
5. Intersinus width nearest widest point (e).
6. Position of widest point: below, above, or at the middle.
7. Number of primary lobes on the right edge of the abaxial side, not including the apex.
8. Number of primary lobes above the middle.
9. Presence of secondary lobes.
10. Length of longest lobe from base of vein (j) and from line between sinuses (k).
11. Indentation index I — $\frac{c-e}{c}$
12. Indentation index II — $\frac{k}{j}$

Leaf silhouettes (FIGURES 4–14) represent only a few examples of each cross. The single white oak leaf is more or less typical for the species, but it obviously may not represent the correct parental type for all crosses. Also, the silhouettes represent only leaf form and should never be taken alone to indicate hybridity.

The following variables were used for acorn analysis: (A) nut length and diameter, (B) cup depth, (C) ratio of A/B, and (D) features of

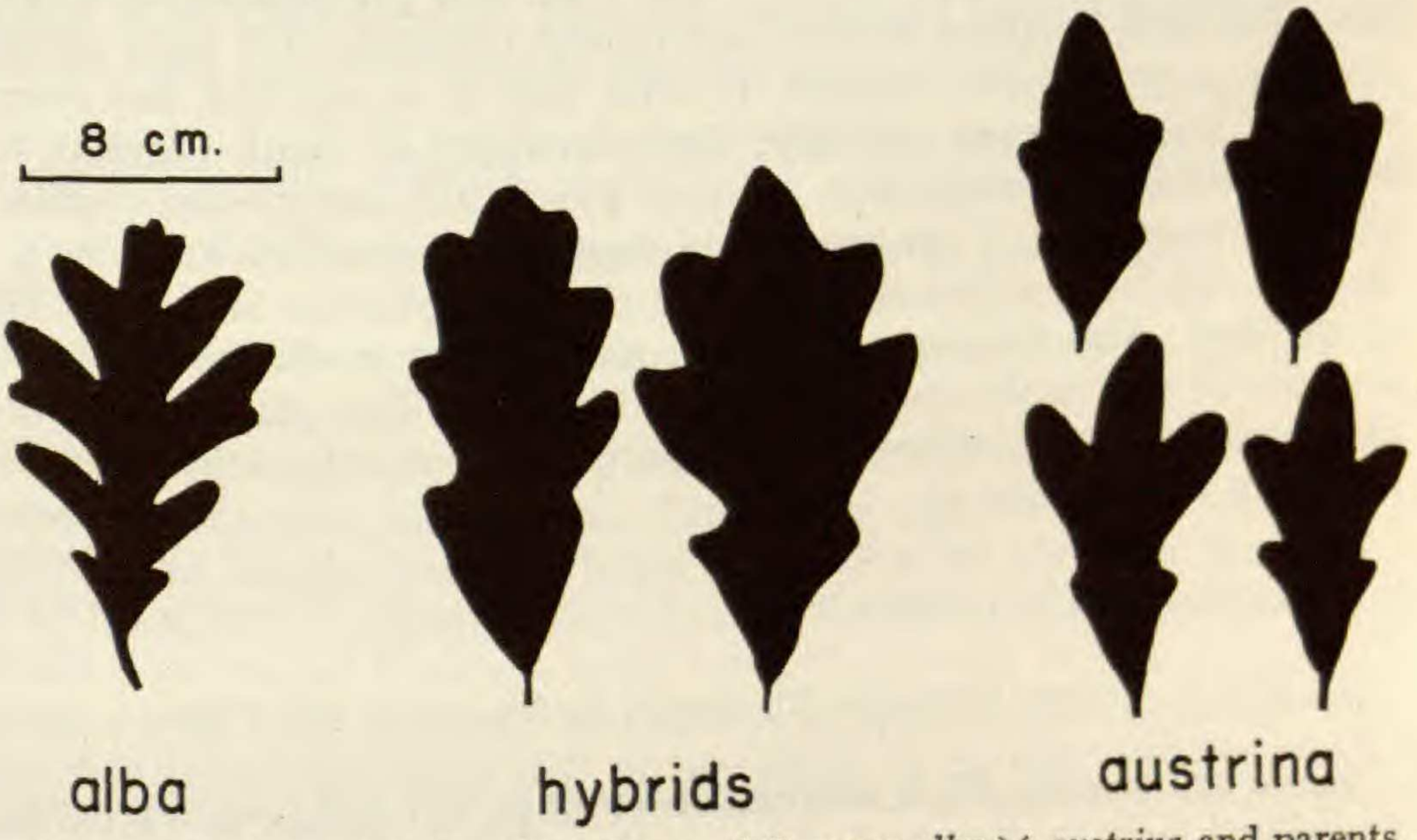

FIGURE 4. Representative leaf forms of *Quercus alba* × *austrina* and parents.

the scales. In some cases the acorn was scored as being like one or the other parent or intermediate, taking all features into consideration.

Twig features such as color, pubescence, form, and size of buds were used as a basis for scoring the twig as being either like one or the other parent or intermediate. Bark of mature trees was scored in a similar manner. Where there was an obvious ecological differentiation between parents in nature, the location of the hybrid was also given a score.

The distribution maps (FIGURES 15, 16) show the location of hybrids identified in the field or from herbarium material. The ranges of the species have been generalized from the detailed maps by Little (1971) in most cases, or very general ranges have been interpreted from various floristic manuals.

### 1. Quercus alba × austrina

The entire complex involving *Quercus austrina* Small, *Q. durandii* Buckl., and *Q. sinuata* Walt. is in need of a critical re-evaluation and field study before definitive judgments can be made regarding hybridization with white oak. Until the taxonomy of this complex is settled, I am for convenience considering only *Q. austrina*, since most of the hybrids involving *Q. alba* are with this segment of the complex. Rehder (1940) included "*Q. a.* × *Durandii*" in his list of white oak hybrids, but Palmer (1945, 1948) did not mention it. I have found a few examples that may be *Q. alba* × *durandii*, on the basis of intermediate lobing and pubescence, but I prefer to withhold judgment until the complex is better understood.

The differences between *Quercus alba* and typical bluff oak (*Q. austrina*) are so subtle that hybrids are difficult to detect. A few herbarium specimens from Mississippi and Florida are tentatively identified as *Q. alba* × *austrina* (FIGURES 4, 15) on the basis of intermediacy of leaf form, color, acorn features, and habitat. There are also populations in lower South Carolina, northern Florida, and central Louisiana that seem to be mixtures of *Q. austrina–durandii*, *Q. alba*, and *Q. margaretta*, but most have not been analyzed critically. One population in South Carolina is discussed under *Q. margaretta.* All such hybrid and introgressed populations are very local. I am tempted to suggest that what we know as *Q. austrina* may have arisen as a result of the past influence of *Q. alba* on *Q. durandii.* The apparent cline from west to east in this complex approaches *Q. alba* in the southeastern United States. This pattern of variation could, however, reflect strong selection and merely a homoplastic similarity with *Q. alba.*

### 2. Quercus alba × bicolor

*Quercus* × *jackiana* Schneider, Ill. Handb. Laubholzk. 1: 202. 1904.

Jack's oak is scattered in distribution (FIGURE 15) and generally occurs as isolated trees in disturbed or intermediate habitats within populations

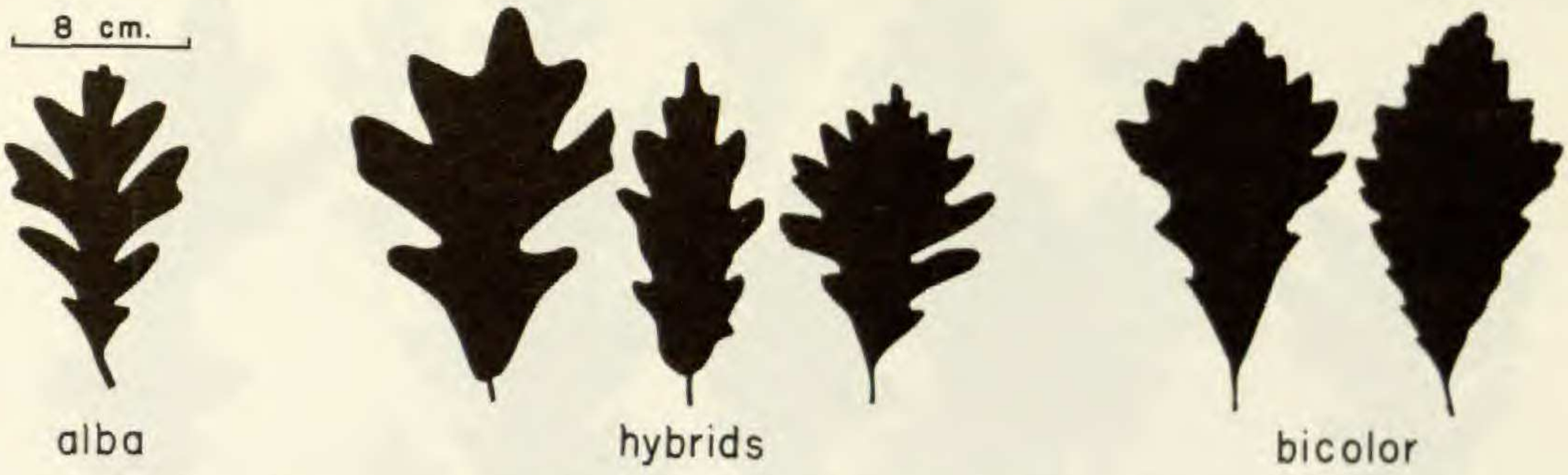

FIGURE 5. Representative leaf forms of *Quercus alba* × *bicolor* and parents.

containing both parental species. It is also quite frequent at the margin of the geographical range of swamp white oak (*Q. bicolor* Willd.).

The leaf outline is more or less intermediate between the leaf outlines of the parental species and is often quite irregular (FIGURE 5). The most distinctive feature is the presence of a mixture of two sizes of branched hairs, a large loose type and a small appressed type (Dyal, 1936), both in less abundance than in typical *Quercus bicolor*.

Acorns collected from a hybrid tree in the Arnold Arboretum were grown in the North Carolina State University greenhouse. The leaves from the seedlings, as well as the parent tree and the typical parental species in the Arboretum, were analyzed with a hybrid index based on number of lobes, indentation index II, general shape, and pubescence; each was scored on a scale from 0 (*Q. alba*) to 4 (*Q. bicolor*). Although the tree was open grown and the pollen parent is unknown, both parental types were in the vicinity. The seedling variation (FIGURE 2B) shows either segregation toward both parents or backcross progeny. The progeny do tend to confirm the parentage of Jack's oak.

This hybrid is infrequent, and gene exchange between the two species seems to be quite limited. Very few populations show more than very limited backcrossing to the more abundant parent species.

### 3. Quercus alba × lyrata

Evidence for this cross of *Quercus alba* with *Q. lyrata* Walt., overcup oak, is limited to a very few scattered locations (FIGURE 15). Palmer (1948) merely listed it among other crosses suspected on the basis of a few specimens at that time.

The hybrids are recognized on the basis of somewhat intermediate leaf shapes, pubescence, and acorns. Leaf lobing appears to be extremely variable but usually shows the broad sinus below the middle of the blade, in addition to a tendency toward having the three relatively large (although more deeply dissected) upper lobes (FIGURE 6). Sparse pubescence on the young twigs and lower leaf surface is characteristic of the hybrids. The thin acorn cup covers half to two thirds of the nut, and the fringe may either be present or not.

Hybrids occur in bottomlands or low woods where the parents are very

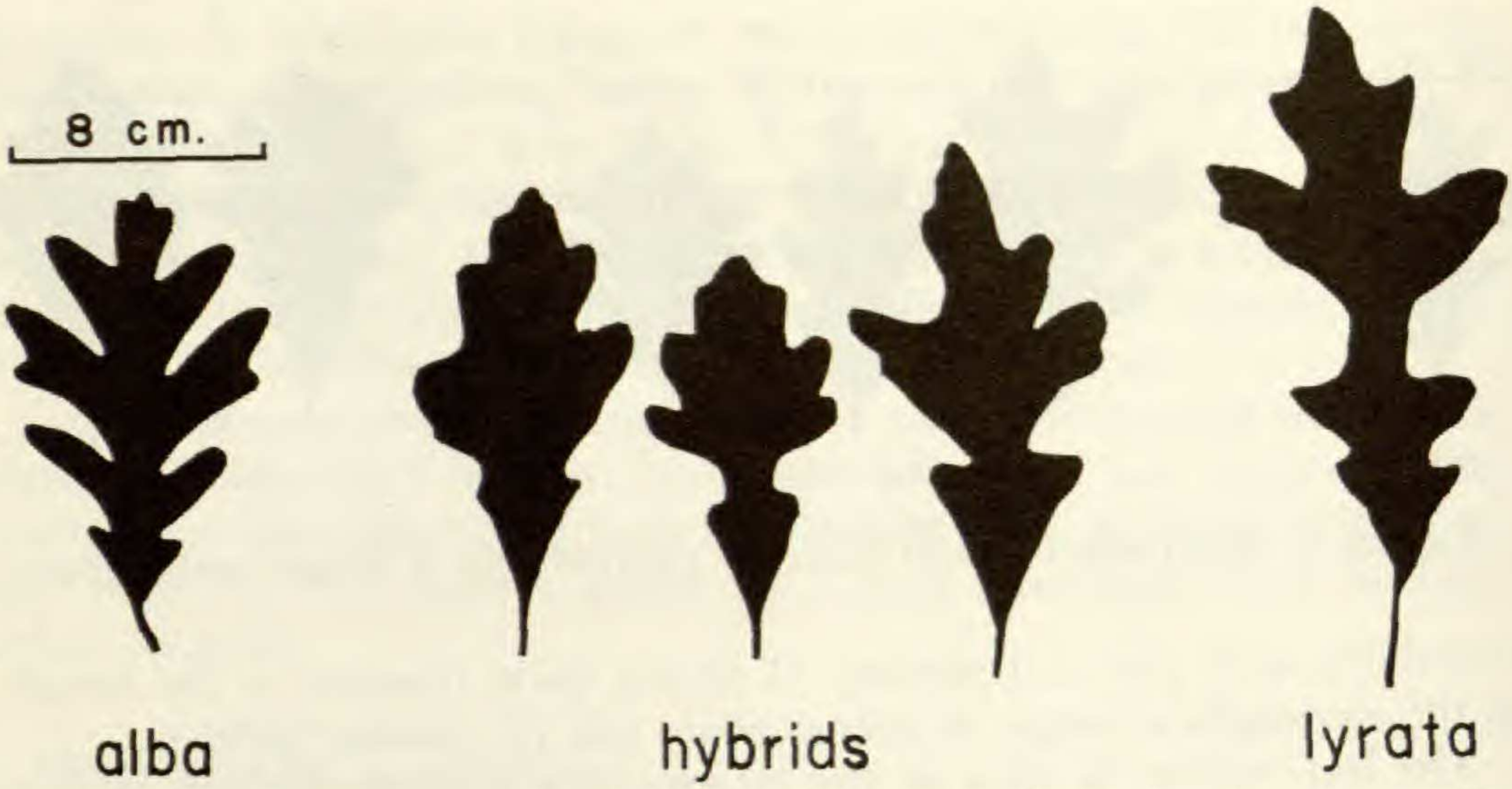

FIGURE 6. Representative leaf forms of *Quercus alba* × *lyrata* and parents.

close to one another and generally where there has been extensive disturbance by past lumbering operations. The hybrids are local, and most backcrossing seems to be with *Quercus lyrata*. Some of the variability of *Q. lyrata* in leaf shape, in pubescence of leaf, twig, and bud, and in depth of acorn cup may reflect a "trickle" of genes from white oak into overcup oak. The influence of overcup oak on the morphology of white oak appears to be very local and negligible.

### 4. Quercus alba × macrocarpa

*Quercus* × *bebbiana* Schneider, Ill. Handb. Laubholzk. 1: 201. 1904.

Bebb oak is one of the most frequent of the white oak hybrids, and it is also one of the good examples of introgression. It occurs in scattered locations (FIGURE 15) within the area of sympatry of white and bur oak (*Q. macrocarpa* Michx.).

Although there are "various degrees of transition between parent species" (Palmer, 1948), the hybrids are fairly easily recognized by the intermediacy of features or the mixture of parental characters. Leaf shapes (FIGURE 7) form a continuum between the parental types, but they usually show at least a tendency toward the broad sinus below the middle of the blade and the massive portion above. The hybrids consistently have some degree of pubescence on the lower leaf surface, and the petiole may be pubescent or glabrous. The acorn cup is generally deeper than in white oak, but the marginal fringe, so characteristic of bur oak, may or may not be present. The bark may be intermediate or more like that of one of the parents. Although the ecological ranges of the parental species are somewhat different, the two plants are frequently close associates and appear to occupy similar sites.

A rather large population near Brighton, Livingston County, Michigan, was analyzed in detail. Samples were taken from 56 trees scattered over

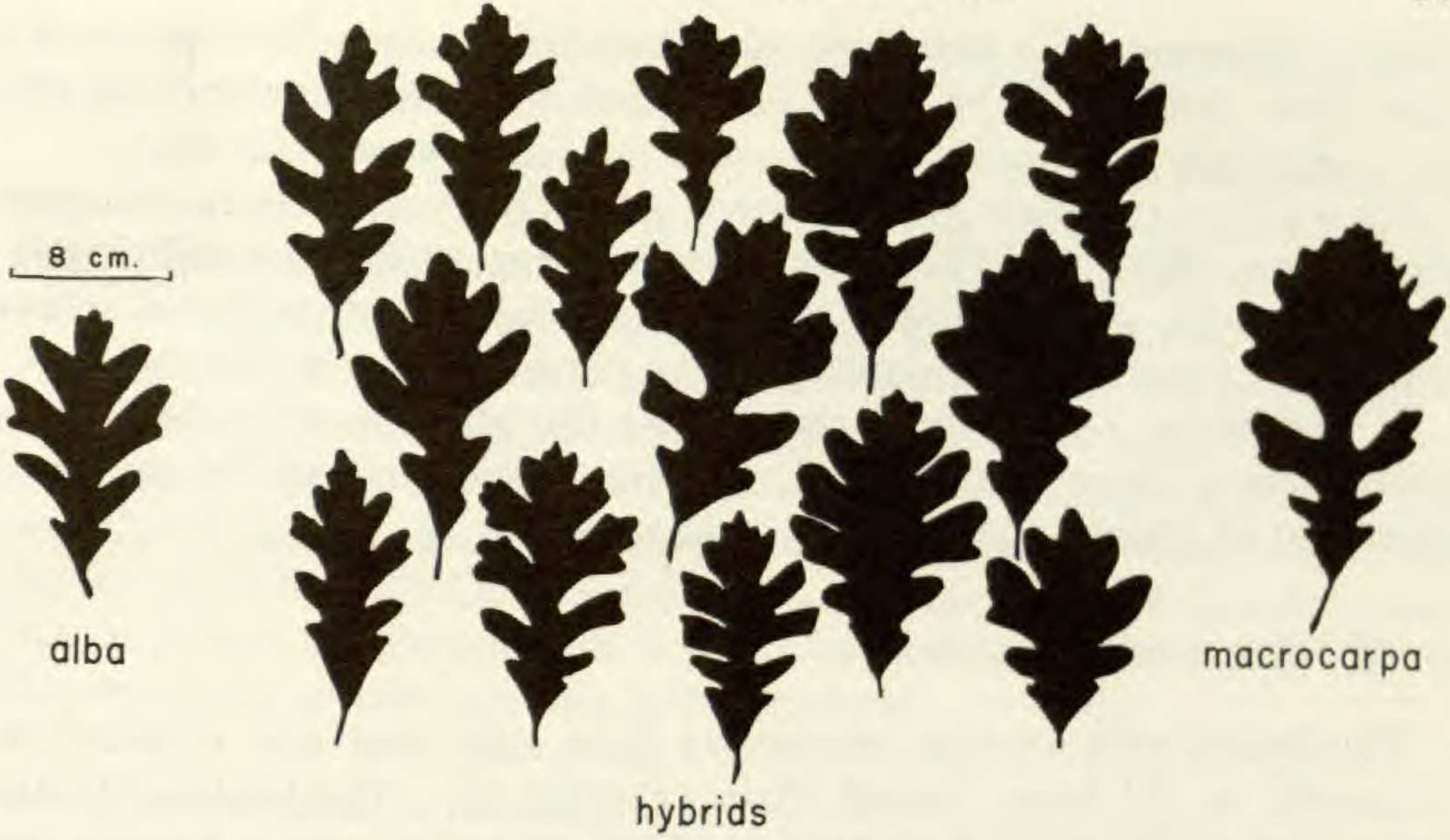

FIGURE 7. Representative leaf forms of *Quercus alba* × *macrocarpa* and parents.

an area of about one square mile. The area was at that time (before construction of two dual-lane highways and a sprawling intersection) covered by an open mixed hardwood forest in small to medium-sized woodlots dissected by pastures and cultivated fields. Some large trees remained along roadsides and in pastures. Much of the area showed signs of extensive disturbance by logging and grazing. Only mature trees greater than 4 inches dbh were sampled. Ten trees of each parental species were sampled from scattered locations in Lapeer and Oakland counties, Michigan. Hybrid indices were constructed using a scale of 0 (*Q. alba*) to 2 (*Q. macrocarpa*) for the following eight diagnostic features: bark (light ashy gray to darker gray and more distinctly ridged), twigs (glabrous to pubescent), acorns (less than 3/4 inches to greater than 3/4 inches, cup less than 1/2 to greater than 1/2 length of acorn, without or with fringe), leaf pubescence (glabrous to densely hairy), and leaf form (oblong to obovate, without and with wide central sinus and massive upper portion).

This hybrid population (FIGURE 3C), in contrast to the typical species, is composed of both parental types plus various hybrid forms. There may be some limited segregation toward both parents, but there is probably more backcrossing, particularly to *Q. macrocarpa,* which is the more frequent parent in the immediate area. This pattern seems rather typical of a number of populations that exhibit limited gene exchange between species. The predominance of forms closer to bur oak is probably due to differential pollination rather than differential selection of seedlings. Presumably any hybrid seedling could compete well in this open, disturbed habitat in which both parental species are well adapted.

Hybrids are nearly always associated with both species. However, a population of hybrids more like bur oak was found near Mora, Kanabec

County, Minnesota. No white oaks were found in the area. The hybrids are large trees, possibly 50 to 75 years old, and white oak has undoubtedly been selectively cut from the area since the hybrids were formed.

Bebb oak exists either as single trees, probably $F_1$ hybrids, or in mixed populations, which could be either hybrid swarms or introgressed populations. Hybrids are localized, and introgression seems to have rather limited influence on the variability of the parent species in the region.

Li and Hsiao (1974) have shown that the phenolic compounds in a hybrid tree growing at the Morris Arboretum substantiate the suspected parentage of *Quercus alba* and *Q. macrocarpa.*

### 5. **Q. alba × margaretta**

The hybrid with *Quercus margaretta* Ashe, sand post oak, is found infrequently in the lower Coastal Plain (FIGURE 15). The habitat of sand post oak is fairly restrictive (Muller, 1952), and white oak generally does not occupy the same sites. Undoubtedly the ecological barrier is very effective where the parental species are close enough for cross-pollination, and an intermediate habitat is necessary for the survival of the hybrid.

This hybrid was included under *Quercus × fernowii* (*Q. alba × stellata*) by Palmer (1948). The collections from Nansemond County, Virginia, which Fernald (1942) considered to be *Q. alba × stellata* var. *margaretta* were cited by Palmer under *Q. × fernowii.* I consider *Q. margaretta* to be a distinct species, and likewise the hybrid with white oak is distinct from *Q. × fernowii.*

The hybrid between *Quercus alba* and *Q. margaretta* is recognized by the more or less shrubby or small tree habit, smaller leaves, large pedicellate branched hairs (in contrast to the sessile branched hairs in *Q. alba × stellata*), and glabrous twigs. Leaf shapes (FIGURE 8) are variable but generally indicate the large lobes of the upper half.

In most cases, these hybrids occur as single individuals or small clones. However, there are populations, particularly in the southwestern part of the range, where presumably reciprocal or unilateral introgression has occurred and heightened the variability of both parental species in the immediate area. A hybrid index for a population in Harrison County,

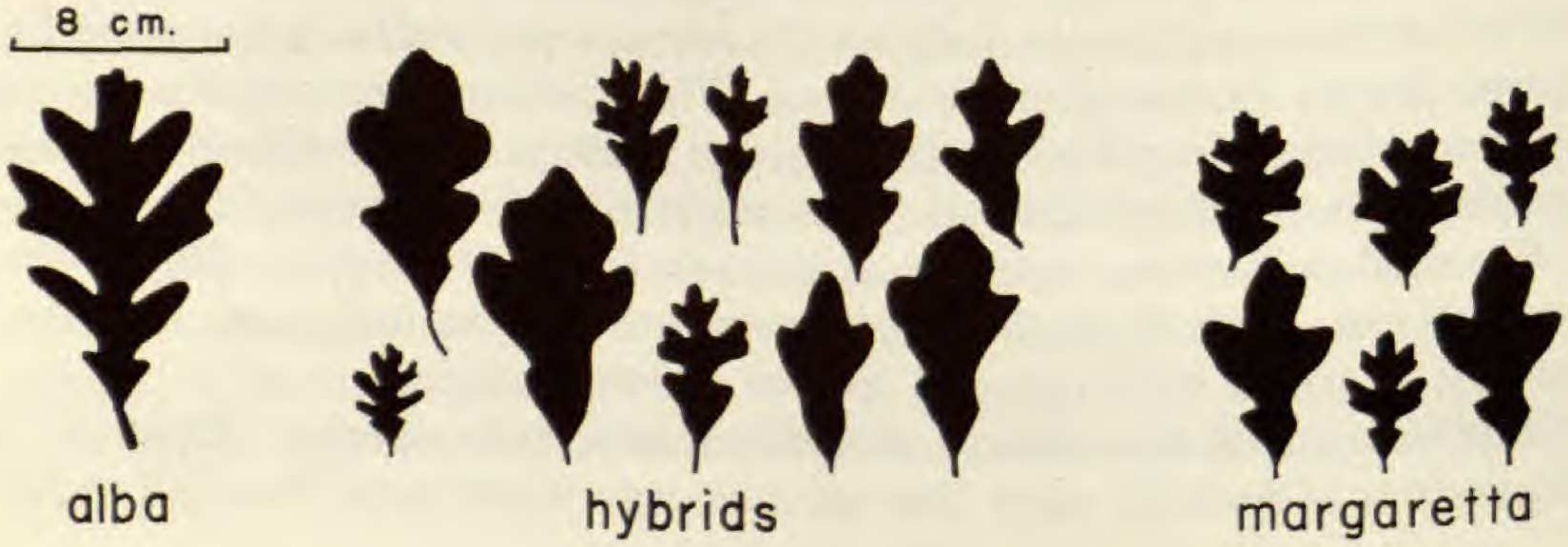

FIGURE 8. Representative leaf forms of *Quercus alba × margaretta* and parents.

Texas would appear quite similar to that in FIGURE 3C, owing to the greater backcrossing to *Quercus margaretta*.

As mentioned under *Quercus alba* × *austrina*, there are populations that appear to be mixtures of *Q. alba*, *Q. austrina*, and *Q. margaretta*. One such population near Bluffton, South Carolina is a mixture of a few large white oaks, infrequent sand post oak, and fairly common bluff oak and hybrids. The hybrid forms are either small single trees (more nearly *Q. alba* × *austrina*) or clones of stoloniferous small trees to eight feet tall. The leaves are mostly like *Q. alba* × *austrina* in shape and texture but have scattered pedicellate branched hairs and occasional larger lobes at the apex typical of *Q. margaretta*. The habitat is a low, sandy, pine flatwood, which has been heavily disturbed in the past by lumbering operations. The influence of this mixture appears to be very local.

## 6. Quercus alba × michauxii

*Quercus* × *beadlei* Trelease ex Palmer, Jour. Arnold Arb. **29:** 16. 1948.

Beadle oak is found rather infrequently in scattered geographical locations (FIGURE 15) and in low woods, on the lower slopes adjacent to floodplains, or in swamps where the ecological ranges of white oak and swamp chestnut oak (*Quercus michauxii* Nutt.) overlap.

This hybrid is fairly easily recognized by the light gray, flaky bark, the more or less intermediate leaf form (FIGURE 9), the sparse pubescence of loose branched hairs, and acorns of more or less intermediate size, the cups with rather coarse, thick, and loosely imbricated scales. The leaf form (FIGURE 9) appears very similar to *Quercus alba* × *bicolor* (FIGURE 5), *Q. alba* × *prinus* (FIGURE 12), or *Q. alba* × *muehlenbergii* (FIGURE 10), and distinction between these four has to be based on other features, such as bark, pubescence, acorns, and ecology. A number of herbarium specimens were found to be mistakenly identified as *Q. alba* × *prinus* (*montana*).

The hybrids seem to exist as individuals in disturbed, intermediate habitats, and there is no evidence thus far of either extensive hybrid swarms or introgressed populations.

The use of the name *Quercus prinus* L. continues to be a source of con-

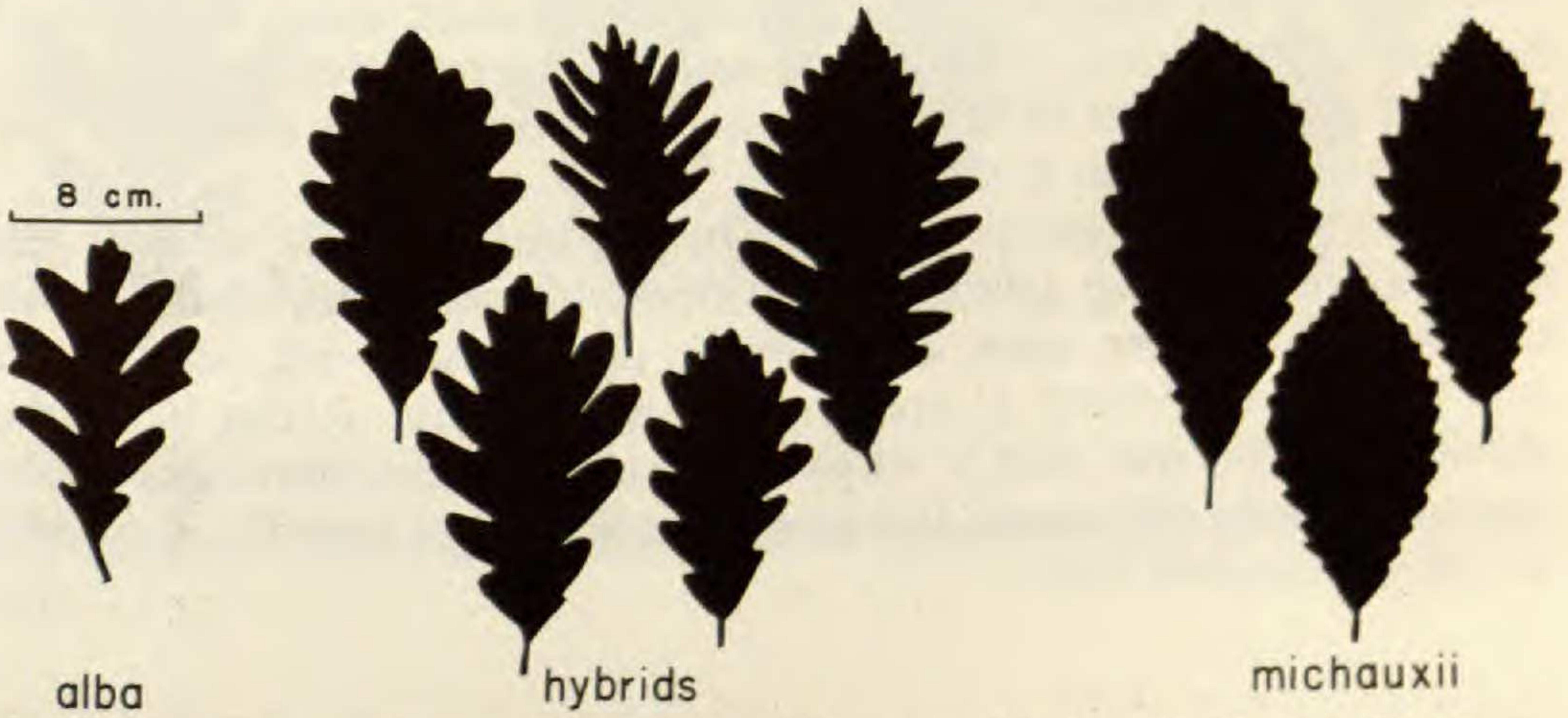

FIGURE 9. Representative leaf forms of *Quercus alba* × *michauxii* and parents.

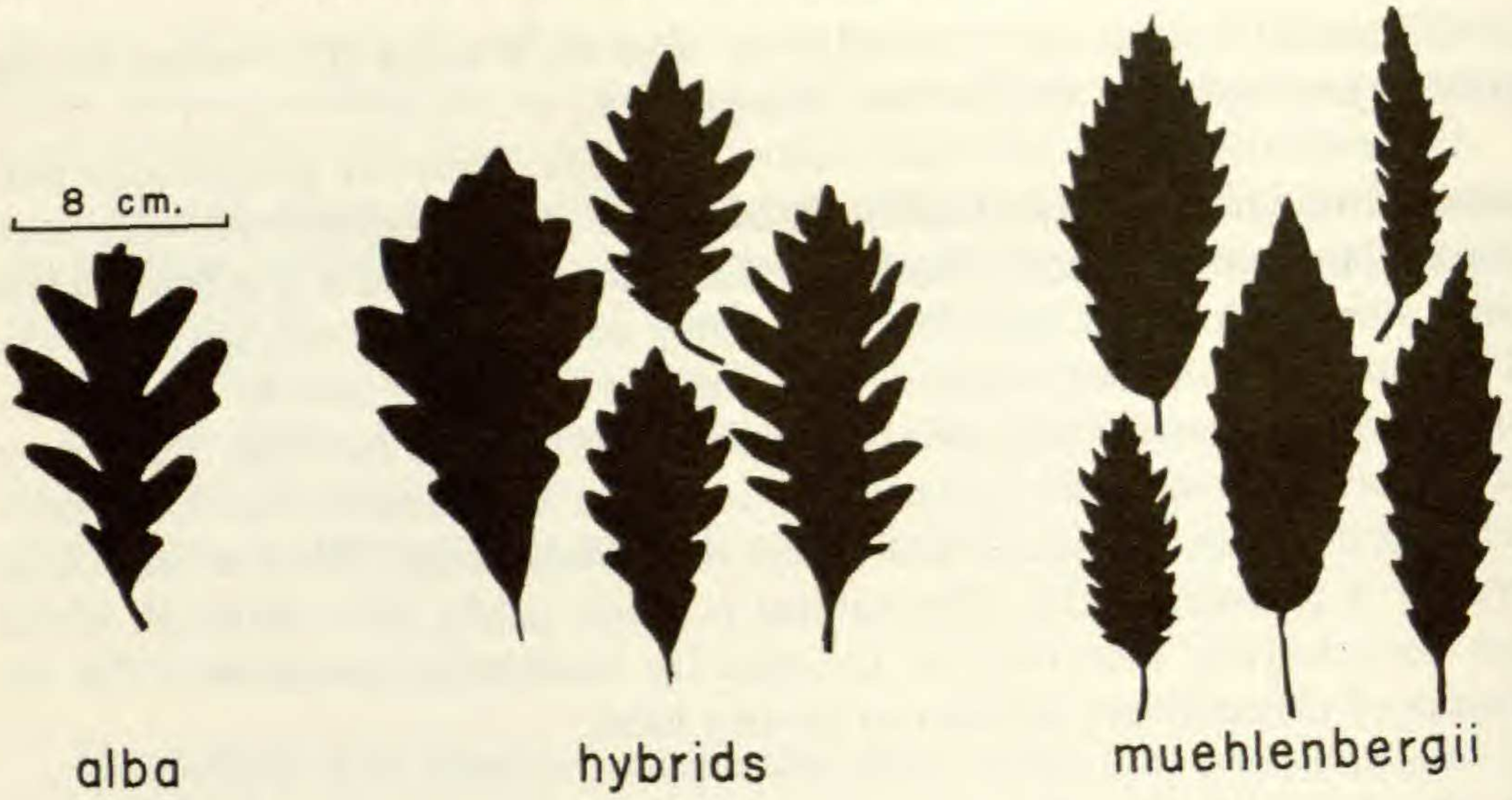

FIGURE 10. Representative leaf forms of *Quercus alba* × *muehlenbergii* and parents.

fusion, and it may be a good candidate for rejection under Article 69 of the *Code*. Standardization of the use of *Q. prinus* for chestnut oak and *Q. michauxii* for swamp chestnut oak did not follow the publication of Little's *Check list* (1953) as was hoped, for many recent publications use *Q. prinus* for swamp chestnut and *Q. montana* Willd. for chestnut oak. C. H. Muller considers the Linnaean type specimen to be the swamp chestnut (Bernard & Fairbrothers, 1967). At this time, no one can be certain of the meaning of the name *Q. prinus* unless it is accompanied by a synonym, common name, habitat, or distribution. However, I prefer, at least for the present, to continue to follow Little (1953) and to use *Q. michauxii* for the swamp chestnut oak and *Q. prinus* for the chestnut oak.

### 7. Quercus alba × muehlenbergii

*Quercus* × *deamii* of some authors; not Trelease, Natl. Acad. Sci. Mem. 20: 14. 1924.

White oak and chinkapin oak (*Quercus muehlenbergii* Engelm.) are frequent associates on calcareous soils, and hybrids between them have been found at the edge of fields or in heavily disturbed woods in scattered locations (FIGURE 16). There is no evidence of extensive introgression, for most hybrids seem to exist either as single trees or at most as a few individuals together in a small area.

This hybrid is recognized primarily by the leaf, which is more or less intermediate in lobing (FIGURE 10), often with the rather sharp points and glandular mucros more characteristic of chinkapin oak, and always with some given density of appressed branched hairs. It can be distinguished from *Quercus alba* × *bicolor* by the lack of the two sizes of hairs mentioned under that cross. It is questionably distinct from *Q.* × *faxonii*, as will be discussed later.

The name Deam oak (*Quercus* × *deamii* Trel.) has often been mistakenly associated with this hybrid cross, since a tree from near Bluffton, Indiana, which was later named *Q.* × *deamii* by Trelease, was originally determined by Sudworth to be *Q. alba* × *muehlenbergii* (cf. Palmer, 1948). Palmer, although he used this binomial for this cross, questioned the parentage of the tree, since seedlings raised from acorns from the type tree included individuals with leaves similar to those of *Q. bicolor*. I collected acorns from *Q.* × *deamii* growing at the Arnold Arboretum and grew them in the North Carolina State University greenhouse for two years. Some leaves had the general shape of *Q. bicolor*, but they all lacked the two sizes of hairs, the lobes were more pointed (like those of *Q. muehlenbergii*), and many had the shape indicative of *Q. macrocarpa*. Bartlett (1951) showed from progeny tests from the type tree that *Q.* × *deamii* represented the cross *Q. macrocarpa* × *muehlenbergii*. The progeny which I grew confirm this, and many herbarium specimens originally identified as *Q.* × *deamii* indicate *Q. macrocarpa* and *Q. muehlenbergii* rather than *Q. alba*. Thus *Q.* × *deamii* applies to *Q. macrocarpa* × *muehlenbergii*, and the cross between *Q. alba* and *Q. muehlenbergii* has no binary name.

### 8. **Quercus alba × prinoides**

*Quercus* × *faxonii* Trelease, Natl. Acad. Sci. Mem. **20**: 14. 1924.

Faxon oak has been identified infrequently from scattered locations (FIGURE 16). Except for generally smaller leaves (FIGURE 11) and a shrubby or smaller tree habit, it is doubtful whether *Q. alba* × *prinoides* can always be distinguished from *Q. alba* × *muehlenbergii*. The leaf often has fewer and shallower lobes, but these features are quite variable. Much of the variation would seem to be due to the intrinsic variation in the parental species, and it is questionable whether the chinkapin oaks represent two distinct species.

There is no indication that this cross leads to any increased variability in the parental species. Hybrids occur rarely, and then usually as indi-

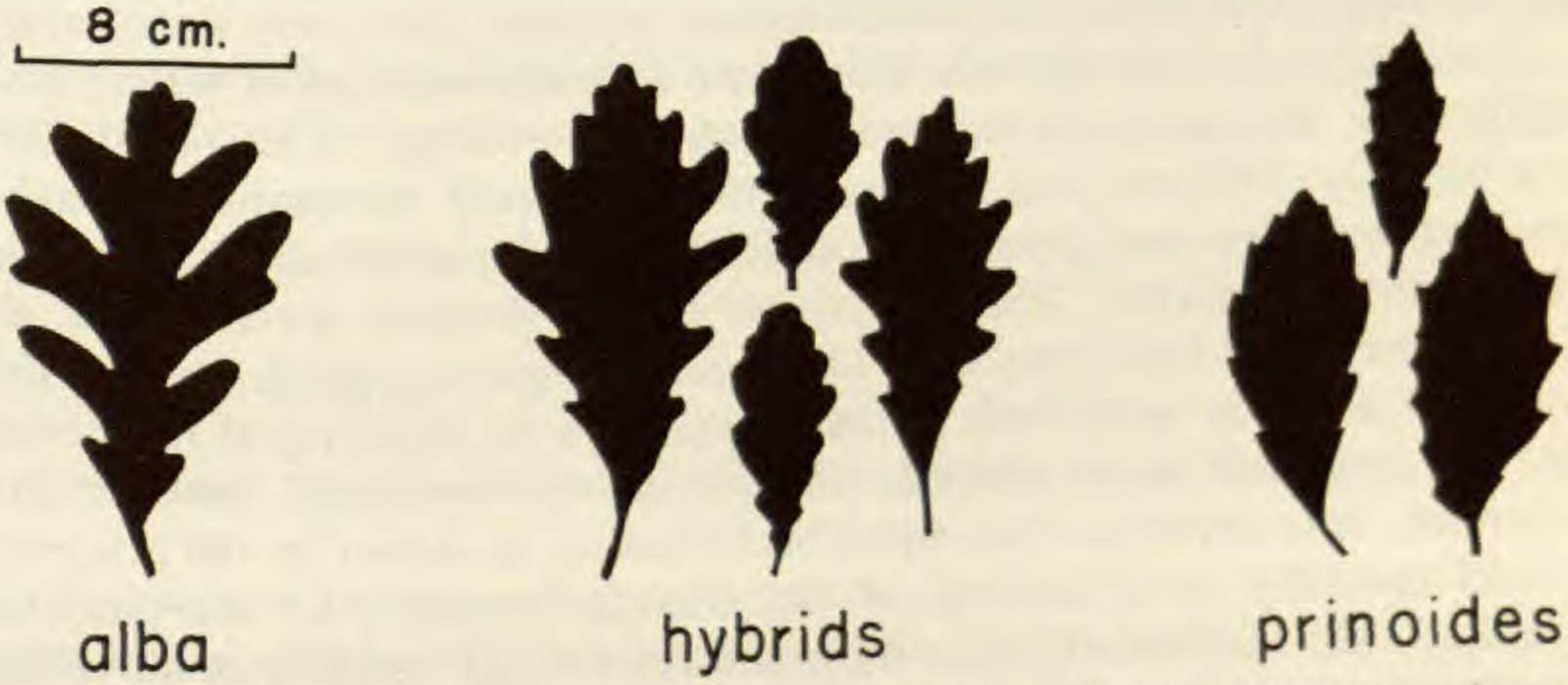

FIGURE 11. Representative leaf forms of *Quercus alba* × *prinoides* and parents.

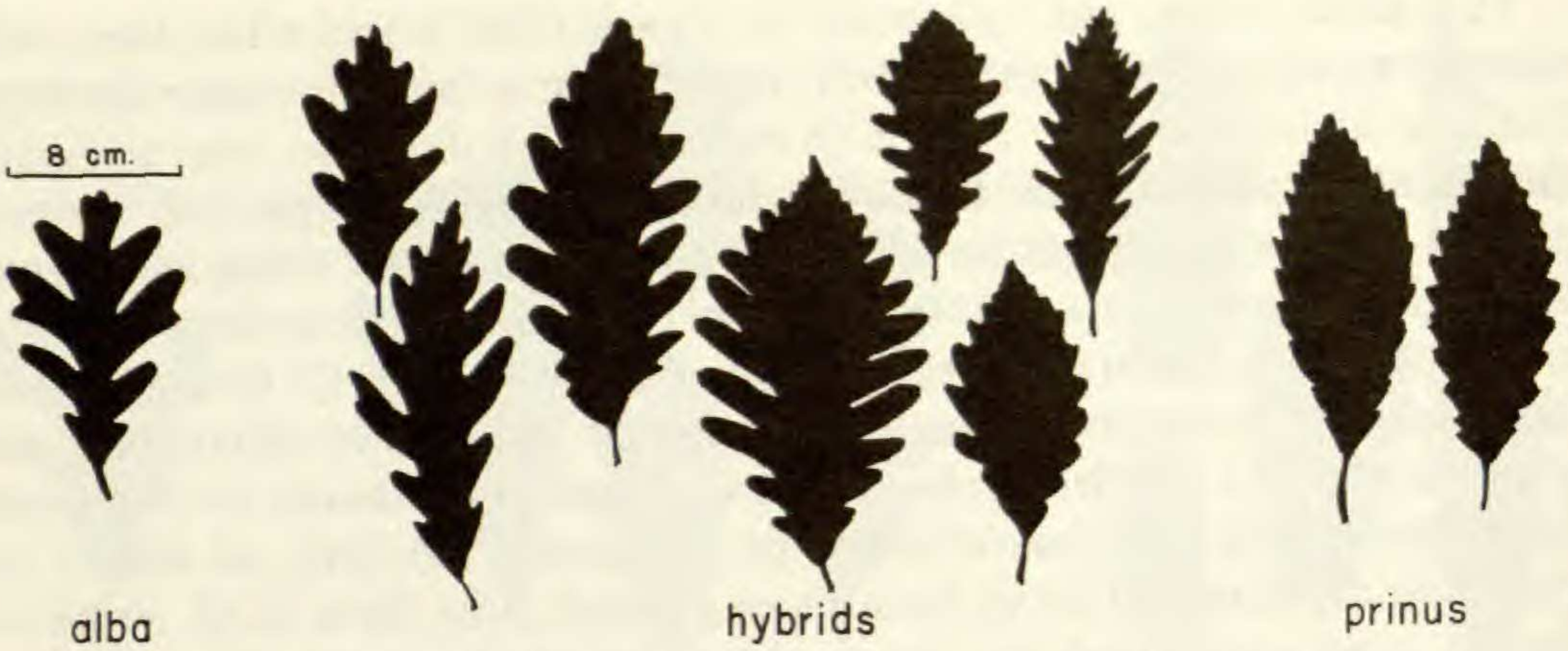

FIGURE 12. Representative leaf forms of *Quercus alba* × *prinus* and parents.

viduals or infrequent backcrosses to the dwarf chinkapin oak (*Quercus prinoides* Willd.).

The map (FIGURE 16) for dwarf chinkapin oak is very general and is probably quite incomplete in some areas.

### 9. **Quercus alba × prinus (montana)**

*Quercus* × *saulii* Schneider, Ill. Handb. Laubholzk. 1: 203. 1904.

Saul oak is not only one of the most commonly found hybrids (FIGURE 16) but is also one of the best examples of introgression among the white oak hybrids. In addition, it is the best known through progeny tests (Allard, 1932, 1949; Ledig *et al.*, 1969) and population analysis of mature trees (Silliman & Leisner, 1958).

This hybrid is easily recognized by the leaf, which has more lobes than white oak but deeper sinuses than chestnut oak (FIGURE 12), by the varying numbers of branched hairs on the abaxial leaf surface, by the intermediate terminal bud sizes, by the more or less intermediate acorn size and nature of the cup scales, by the intermediate bark, and by its occurrence generally in an intermediate and disturbed habitat where the parental species overlap in their ecological ranges.

The various studies cited above indicate a limited amount of selfing and segregation and a significant amount of backcrossing. The population analyzed by Silliman and Leisner (1958) showed predominant backcrossing with *Quercus prinus* or possibly a selection for these types by the particular habitat. The analysis of hybrid progeny by Ledig *et al.* (1969) indicated backcrossing to both parental species, which may be the expected situation when both parental types are in about equal frequency in the area and when natural selection of the seedlings has not yet occurred. Any deviation from equal backcrossing, as shown by the progeny, would normally be a function of the relative frequency of the parental species in the vicinity. Further deviation from equal numbers of surviving seedlings and mature trees would be a function of natural selection. This model assumes no differential intrinsic barrier to backcrossing.

A population of Saul oak in Reedy Creek Park, west of Raleigh, North Carolina, was analyzed, since it appeared to have hybrids that approached both parental species. The habitat is a rocky northeast- to northwest-facing slope, with *Quercus alba* in the ravine and lower part of the slope and *Q. prinus* on the ridge and upper part of the slope. The hybrids occur throughout the slope, but they are more abundant in the mid-section. Both parental species are present in large numbers, and the habitat appears intermediate and open enough to accommodate all hybrid forms. Forty trees from a transect perpendicular to the contours were selected as probable hybrids on the basis of morphology. For a comparison, samples were taken from eight white oaks from the North Carolina State University Schenck Forest, northwest of Raleigh, and eight chestnut oaks from Hemlock Bluff, southwest of Raleigh. Saul oak is not found in these two locations.

The pictorialized scatter diagram of these populations (FIGURE 3E) probably indicates a more or less equal backcrossing to both parental species, although there may also be some segregation products included. This location is obviously capable of maintaining various products from reciprocal introgression.

This introgressant population at Reedy Creek covers an area of about 70 acres, and the major influence from the gene exchange seems fairly well restricted to that immediate area. A subtle "trickle" of genes from one species into another would be very difficult to detect, although it undoubtedly is occurring. There is certainly no obvious heightened morphological variation in either *Q. alba* or *Q. prinus* in the region as a result of the scattered populations of Saul oak. The heightened ecological variation, although difficult to analyze, may be more extensive.

Several populations of Saul oak in other areas show introgression with the predominant tendency toward backcrossing to the more abundant parental species. In all cases the hybrids are found in intermediate habitats that have been opened up by fire, logging, grazing, highways, or powerline construction.

The name *Quercus prinus* L. is at present meaningless without either an associated synonym, common name, habitat, or distribution, as discussed under *Q. alba* × *michauxii*. Although use of the name *Q. montana* Willd. is less ambiguous and possibly correct, I continue to follow Little (1953) and to use *Q. prinus* until the name is formally designated as a *nomen ambiguum* or officially designated as correct for one of the species.

## 10. Quercus alba × robur

*Quercus* × *bimundorum* Palmer, Jour. Arnold Arb. **29**: 18. 1948.

The hybrid between white oak and the English oak (*Quercus robur* L.) was first found in 1923 in Jamaica Plain, Massachusetts, and has since been found only in a few locations in eastern Massachusetts and southeastern Pennsylvania (Palmer, 1948). The habitats have been woods in

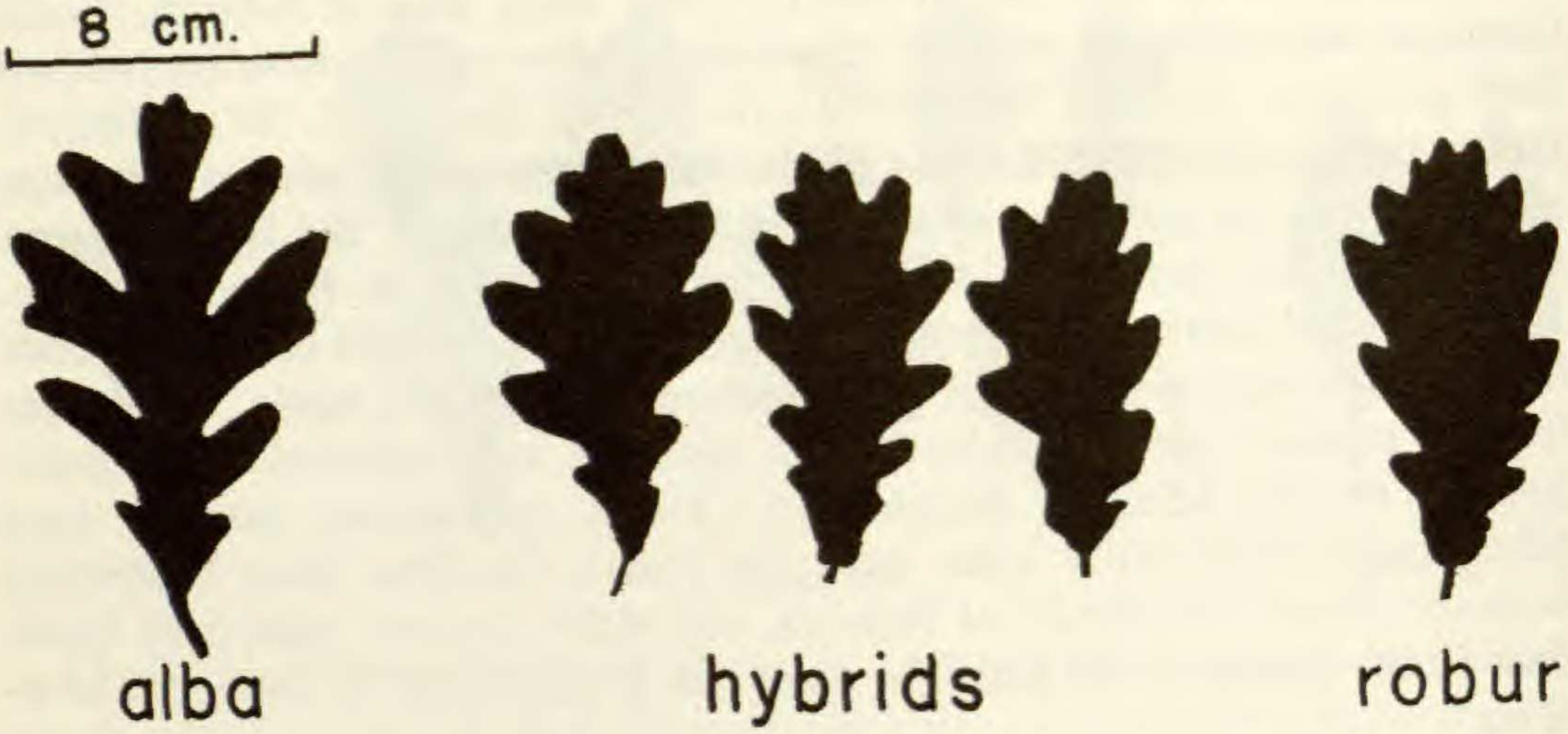

FIGURE 13. Representative leaf forms of *Quercus alba* × *robur* and parents.

or near cities in which the English oak is cultivated. Although none of the populations in the immediate areas have been analyzed, any backcrossing would probably be with the native and more abundant white oak.

This hybrid can be recognized by the bark, which is medium gray and only slightly flaky or furrowed, and by the leaves (FIGURE 13), which are glabrous and usually smaller than those of typical white oak and which show a tendency toward a truncate or narrow cordate base and a very short petiole. The number of leaf lobes and degree of dissection are too similar in the parental species to be used for identification.

An artificial cross between white oak and English oak was reported by Piatnitsky (1960). Schreiner and Duffield (1942) discussed a similar cross and gave an interesting account of metaxenia, in which the pollen parent (*Quercus robur*) had a delaying effect on the maturity of the hybrid acorns. Artificially produced hybrids are very similar to the putative hybrids identified in nature. The progeny of hybrid trees, grown at the North Carolina State University greenhouse, also substantiate this cross.

### 11. Quercus alba × stellata

*Quercus* × *fernowii* Trelease, Natl. Acad. Sci. Mem. **20**: 15. 1924.

The cross known as Fernow oak is of scattered occurrence (FIGURE 16). It can be recognized by bark that is lighter and less ridged than in *Quercus stellata*; twigs that are pale and canescent or with scattered hairs; short-stalked acorns with shallow cups and smooth close scales; leaves that are more or less pubescent below with large, erect, sessile, branched hairs and sometimes with minute stellate hairs; and leaf lobes (FIGURE 14) generally indicative of the large wide lobes near the middle of post oak leaf blades. It can be distinguished from *Q. alba* × *margaretta* by the larger leaves, sessile rather than pedicellate branched hairs on the abaxial leaf surface, pubescent twigs, and tree form.

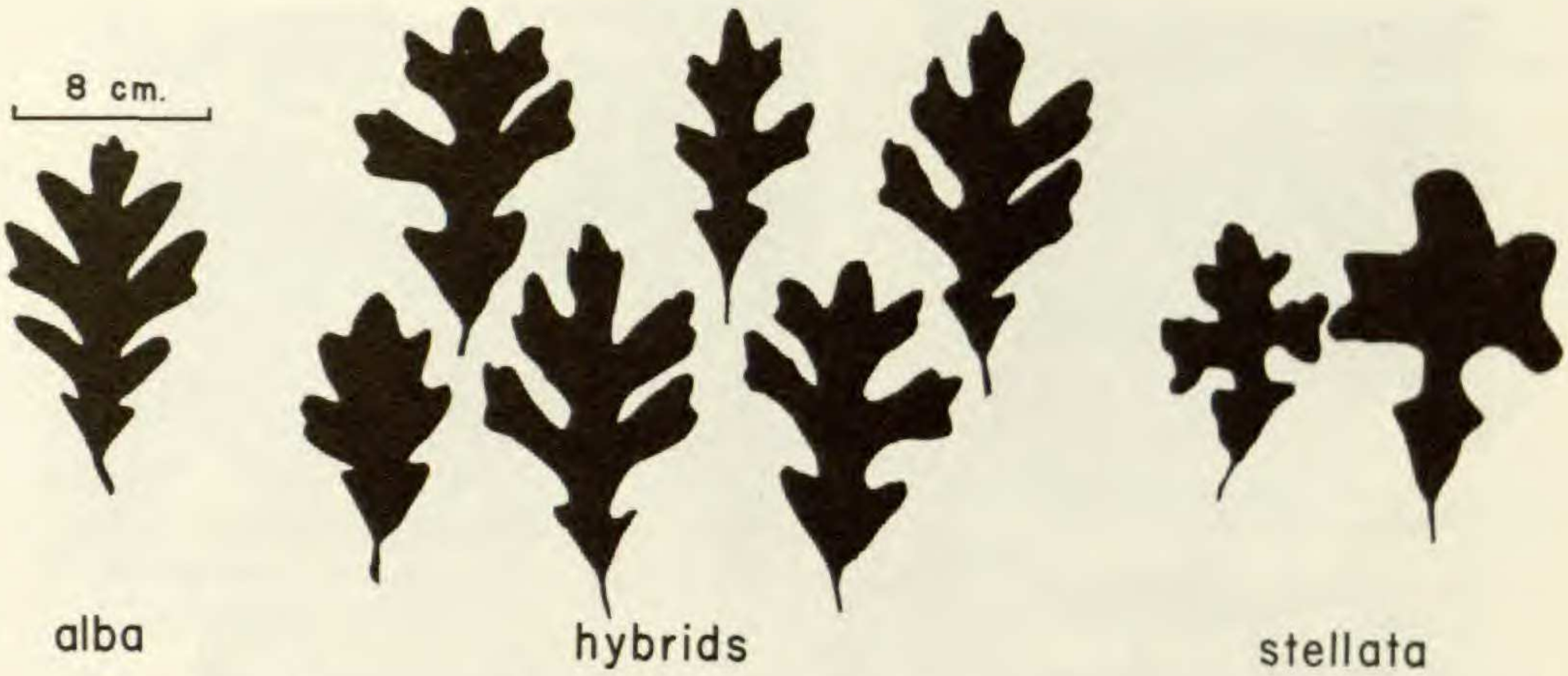

FIGURE 14. Representative leaf forms of *Quercus alba* × *stellata* and parents.

The hybrids generally occur in open, cut-over areas where the parental species are rather closely associated. Intermediate soil conditions are necessary in less disturbed areas. The hybrids are few in number in many localities, but there are some populations in eastern Texas and southeastern Oklahoma that show rather extensive introgression of *Quercus alba* into *Q. stellata* Wang. This is at the margin of the white oak range, so backcrossing could be expected to be to *Q. stellata*.

Samples were taken from a population of 25 mature trees over 4 inches dbh along the eastern edge of Bland Lake, San Augustine County, Texas. A hybrid index was constructed using a scale of 0 (*Quercus alba*) to 2 (*Q. stellata*) for the following four diagnostic features: bark (light ashy gray and flaky — intermediate — reddish brown and longitudinally ridged), twig pubescence (glabrous — scattered hairs — pale and canescent), leaf pubescence (glabrous — scattered branched hairs — densely hairy), and leaf form (even lobing — intermediate — large, wide lobe above middle). All features seemed to vary independently, and from the pattern of variation shown by the population (FIGURE 3D), I suspect a predominance of backcrossing to post oak and possibly some segregation. This pattern seems fairly typical of a number of populations in the southwestern part of the range of *Q. alba*. The white oak of the region shows little influence from this gene exchange away from the local sites of introgression.

### Additional crosses — expected and artificial.

Some three-way hybrids among the eastern white oaks undoubtedly exist, but since there are few qualitative characters by which the parent species can be recognized, it is difficult to detect such crosses. Three-way hybrids in *Aesculus* (Hardin, 1957) were easily identified because of distinct qualitative parental features. Tucker (1961) recognizes characters of three or more species in the *Quercus undulata* complex. One example in the east is the *Q. alba–austrina–margaretta* complex mentioned earlier. A specimen from Ashley County, Arkansas, with leaves like those of *Q. alba* × *lyrata*, but with acorns (attached to the twig) more like those

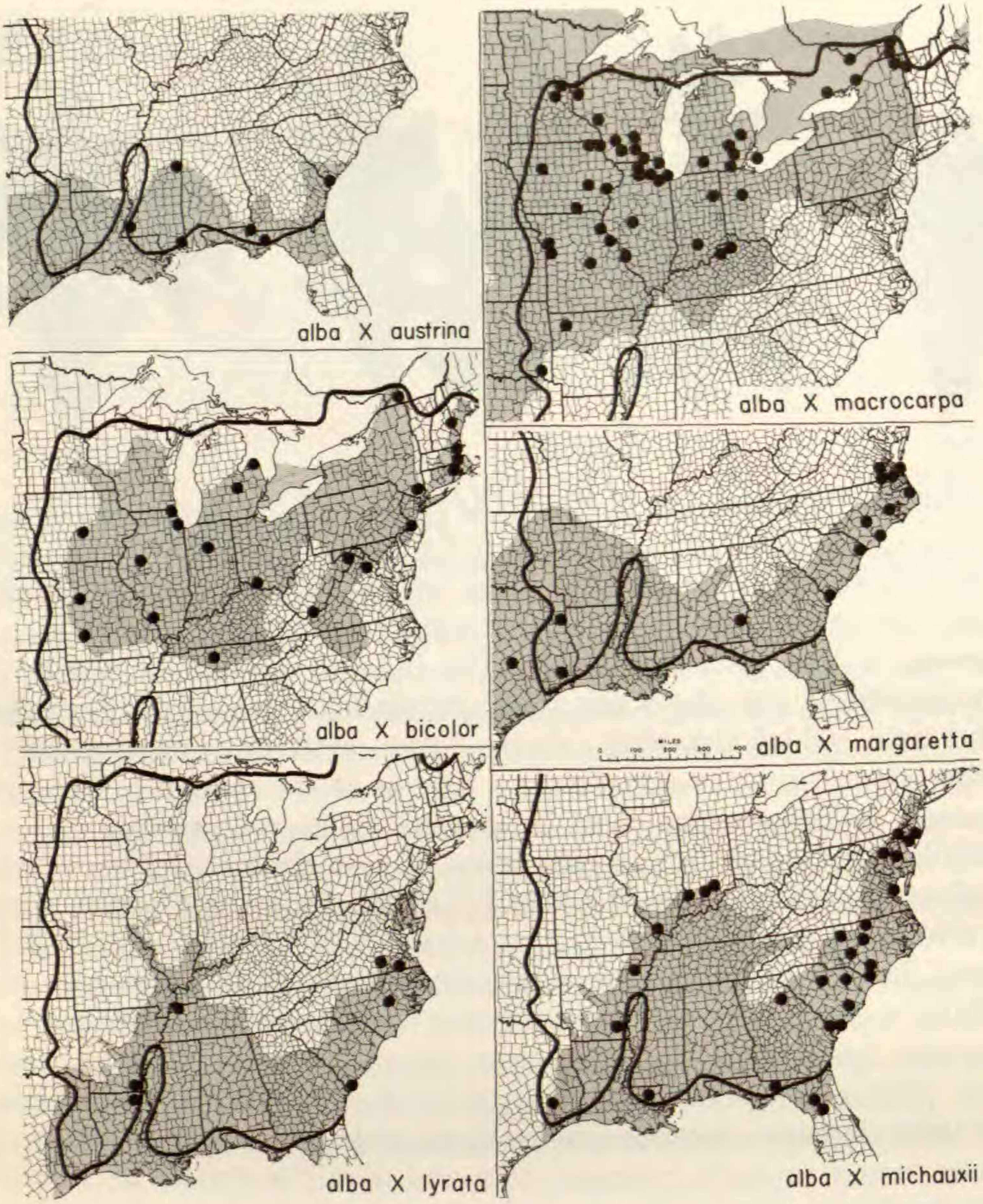

FIGURE 15. Distribution of hybrids (dots) between *Quercus alba* (heavy line) and *Q. austrina*, *Q. bicolor*, *Q. lyrata*, *Q. macrocarpa*, *Q. margaretta*, and *Q michauxii* (shading).

of *Q. michauxii*, may also indicate a mixture of these three species in a low woods. In addition, progeny grown in the North Carolina State University greenhouse from acorns collected at the Arnold Arboretum from a *Q.* × *bimundorum* (*Q. alba* × *robur*) showed a distinct tendency toward *Q. bicolor* in leaf form and pubescence. This could be either the result of crossing there at the Arboretum or a reflection of a three-way parentage of that particular tree. Since a number of oaks are more or less sympatric in many areas, I would certainly suspect that there must be other examples of some limited amount of crossing between three or more parental species.

Within the range of *Quercus alba*, there are four other species of subg. QUERCUS that may be expected to cross with it (FIGURE 1). They are *Q. chapmanii* Sarg., *Q. oglethorpensis* Duncan, *Q. virginiana* Mill., and *Q.*

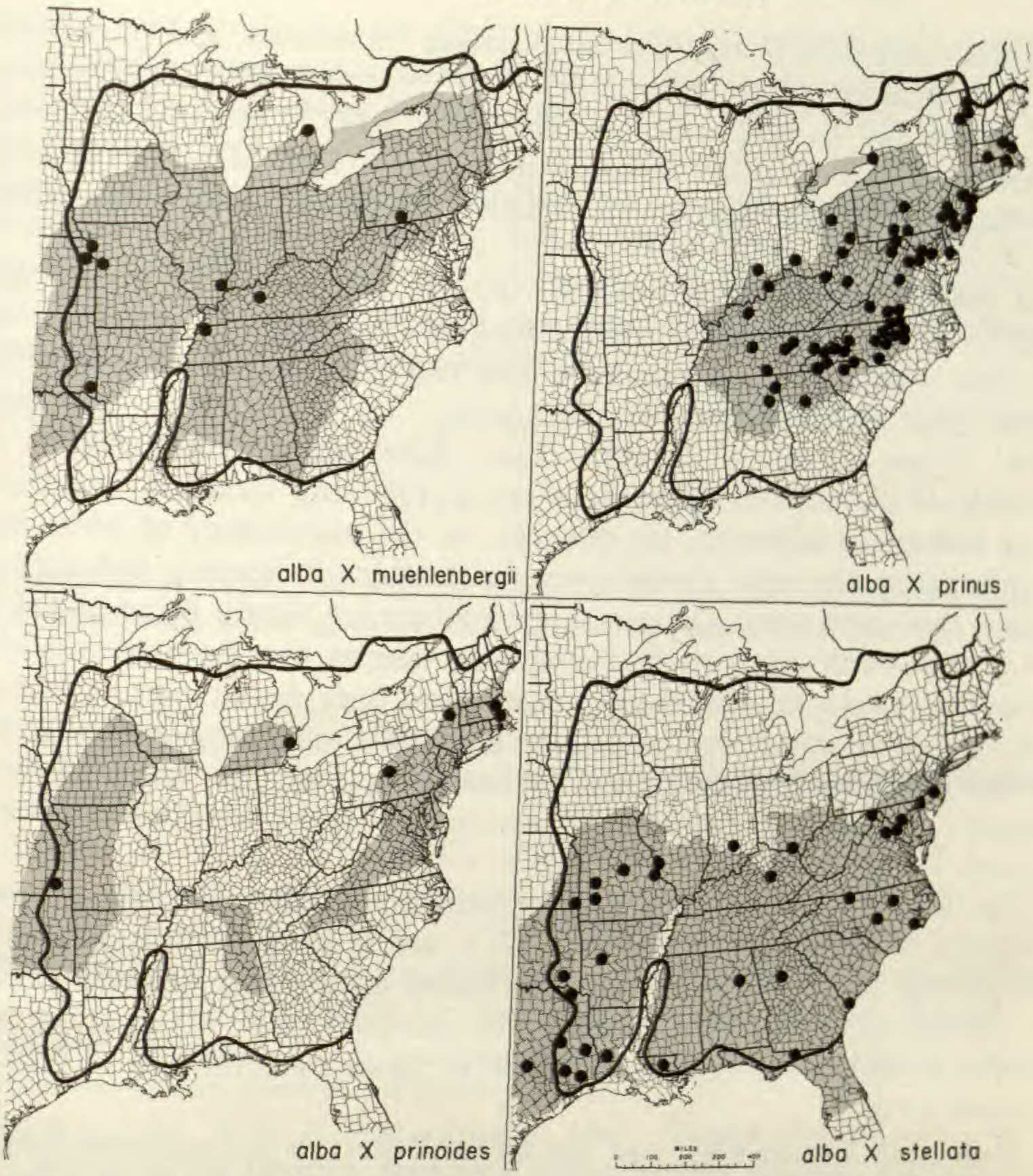

FIGURE 16. Distribution of hybrids (dots) between *Quercus alba* (heavy line) and *Q. muehlenbergii*, *Q. prinoides*, *Q. prinus*, and *Q. stellata* (shading).

*minima* (Sarg.) Small. Hybrids with Oglethorpe oak in particular should be sought, since it is so closely sympatric with white oak.

Piatnitsky (1960) reports the artificial crosses *Quercus alba* × *suber* and *Q. alba* × *macranthera*. Both species are European members of subg. QUERCUS.

## DISCUSSION

The oaks have long had a reputation for being a taxonomically difficult genus owing to intrinsic variability plus frequent hybrids. This survey of hybridization and introgression among the eastern white oaks indicates that although *Quercus alba* crosses naturally with eleven other species, the hybrids are generally quite local single trees and are infrequent in comparison to the abundance of the species in the deciduous forests of eastern North America. Rather extensive hybrid swarms or introgressed populations occur only with *Q. macrocarpa*, *Q. prinus* (*montana*), and *Q. stellata*, and even these are generally localized. The great variability in *Q. alba* is most often due to ecophenic, ecotypic, and random genetic variances (Baranski, 1975). Neither Baranski nor I agree with Minckler (1965), who thinks that hybridization may mask evidence of races within white oak.

As pointed out by Irgens-Moller (1955), "hybridity [in oaks] apparently seldom affects the distinctness of the species." My use of the term "syngameon" in FIGURE 1 does not imply unlimited and widespread gene exchange between the species. To the contrary, the gene "flow" is but a "trickle" in most cases. Even where hybrid swarms or introgressed populations exist, the effect is still fairly localized, and there is no widespread influence, for example, on the morphology of white oak by genes from the other eleven species with which it crosses. Although in certain cases new genes and gene combinations are slowly being added to the genetic architecture of the introgressed species, the essential integrity is not destroyed. All species have maintained their distinctness in face of this local "contamination," and I see no justification for considering the entities anything less than good taxonomic species. In terms of their biology, they can be considered "semi-species" composing a syngameon (Grant, 1971).

The highly localized gene flow appears to be characteristic of most instances of introgression (Heiser, 1973), and it is in marked contrast to the pattern of dispersed introgression found in *Aesculus* (Hardin, 1957) or *Aronia* (Hardin, 1973), where the morphological influence of one species is detected sometimes hundreds of miles from the site of original hybridization.

It appears that in white oak the greatest effect of introgression may be on the ecology of the species. The broad ecological amplitude may be due to some extent to "ecological genes" acquired from other species. If it is assumed that the morphological features used in distinguishing species are governed by relatively few genes (Stebbins, 1950), while ecological adaptation is controlled by numerous genes, this differential flow of "ecological" versus "morphological" genes may be entirely plausible. The question raised earlier of whether the broad ecological amplitude is a cause or a result of introgression is still unanswered, and without knowledge of the original geographical and ecological ranges of the species, we can only speculate on the significance and origin of the broad ecological diversity seen today in *Quercus alba*.

Also unanswered is the question of the identity of the isolating mechanisms which are so effective among the white oaks. The various barriers have been discussed by Stebbins *et al.* (1947), Muller (1952), Tucker (1963), and others, and actually several mechanisms may act together or in sequence. Without definite information on possible incompatibilities, I suspect that ecological isolation is one of the most important means by which so many related white oak species can co-exist in eastern North America in spite of genetic compatibility. I also suspect that strong natural selection limits the extent of the introgressants that are produced.

In recent years introgression as an explanation of certain patterns of variation has been called into question (Heiser, 1973). In view of (1) the geographical and ecological locations of the putative hybrids, (2) their close association with the parental species, (3) the nature of the association of characters within the hybrid populations, (4) study of the progeny from hybrid trees, and (5) the close similarity between artificially produced and natural hybrids, I am satisfied that localized introgression does occur among the eastern white oaks.

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